



Taxonomic and genetic confirmed findings of snow crab (*Chionoecetes opilio*) larvae in the Barents Sea

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Abstract

The snow crab (*Chionoecetes opilio*) is an Arctic cold-water species native to the northwestern Atlantic Ocean and the northern Pacific Ocean. During the recent decades, a population has established in the Barents Sea. Several aspects of the snow crabs' biology in this area have not been described, including time of hatching, intermoult duration of the different larval stages and larval distribution. Insight into the early-life stages might increase the understanding of the population's dynamics and further spreading in the Barents Sea as well as inform basis for making monitoring and management decisions. The present study investigated the presence and developmental stage of snow crab larva in plankton samples obtained in the central Barents Sea during a research survey in June and July 2019. Presence of snow crab larvae was confirmed through taxonomic and genetic identification. All larvae were identified as zoea I, which gives an indication of the timing of the hatching period. Morphological measurements coincide well with those reported in studies from the species native distribution range. No larvae of native *Hyas* spp. were found and overlap in temporal and spatial distribution is discussed. The study provides important information for development of further research into the biology of the snow crab in the Barents Sea.

Keywords DNA barcoding · Hatching · Invaders · Morphology · Phenology · Resource · Zoea

Introduction

The Arctic benthic snow crab (*Chionoecetes opilio*) has a complex life cycle passing through several ontogenetic developmental stages before maturing to adult specimens. The first sensitive period starts with hatching of the ripe eggs and release of planktonic larvae into the water column. Survival of larvae depends on temporal and spatial overlap with adequate densities of suitable prey and favourable temperatures linked with optimal vertical stratification and ocean currents (Houde 2009). Larval survival, the ability to find suitable settlement sites and the risk of predation are all impacted by the duration of the planktonic phase (Rumrill 1990).

Snow crab is naturally distributed in cold waters in the northwestern Atlantic Ocean and in the northern Pacific

Ocean. In 1996 five specimens were found in the Barents Sea, outside its natural distribution range (Kuzmin et al. 1999), and the population has since expanded rapidly both in geographical distribution and abundance in the Barents and Kara Seas (Alvsvåg et al. 2009; Agnalt et al. 2011; Zimina 2014). The population is now widely distributed across the Barents Sea continental shelf (Fig. 1). It is established as a self-reproducing population, implying suitable conditions for all life stages in the area. Fecundity studies from the central part of the Barents Sea documented that egg production is consistent with other studies for the same species in its native distribution range (Danielsen et al. 2019).

The larval phase of snow crabs consists of three pelagic stages, zoea I, zoea II and megalopa. The duration of the larval phase is three to four months, depending on temperature (Ouellet and Sainte-Marie 2018). In the snow crab's native distribution range, hatching season varies from late winter to summer. For example, in the southeastern Bering Sea and in northwestern parts of the Gulf of St. Lawrence, hatching is known to start as early as April (Incze et al. 1987; Sainte-Marie 1993), but can also start later depending on ocean temperature (Landeira et al. 2018). Kon et al. (2003) reported hatching from February to April with a peak in

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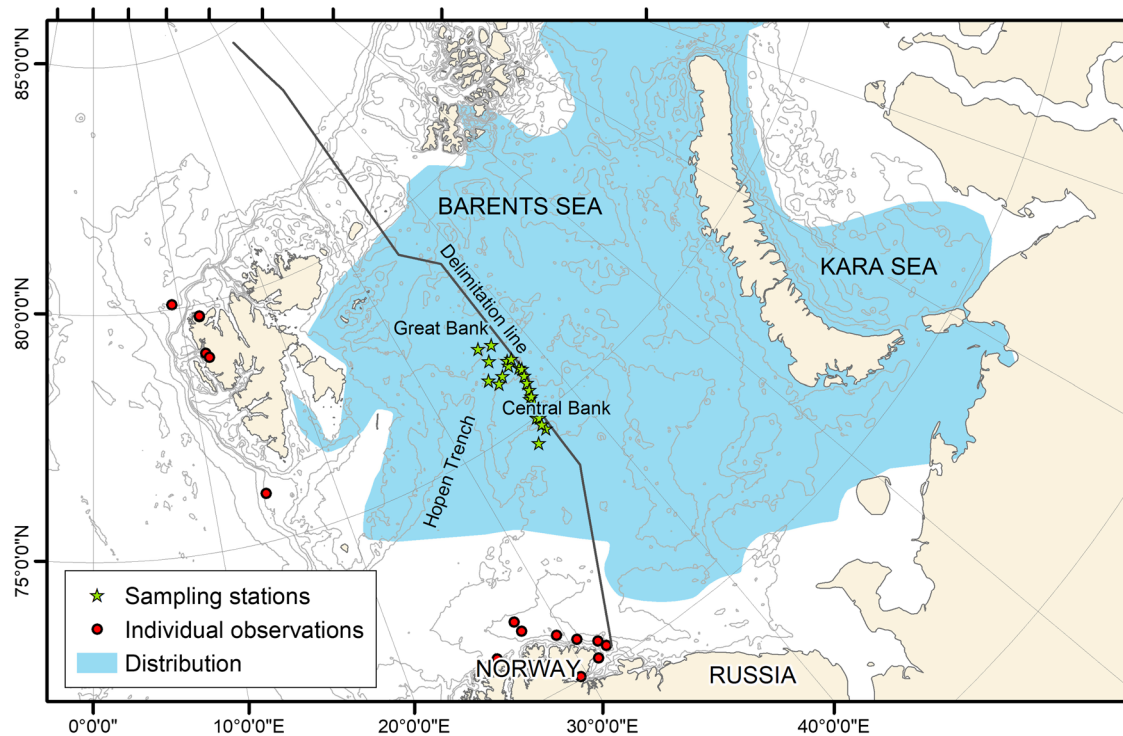


Fig. 1 Distribution of snow crab (*Chionoecetes opilio*) in the Barents and Kara Seas (blue shaded area) based on data obtained from various surveys conducted by the Institute of Marine Research and Polar branch of Russian Federal Research Institute of Marine Fisheries and

Oceanography, as well as information given in Zalota et al. (2018). Observations of individual snow crab outside of the contiguous distribution area are marked with red dots

March in Wasaka Bay in the Sea of Japan. In east Sakhalin and west Kamchatka (Sea of Okhotsk) hatching occurs later, in June and July. In Sakhalin waters, zoea I and II were found in plankton samples in June and July, at water temperatures between 0.7 and 12.7 °C. In Kamchatka waters, high densities of zoea I were observed in early June and zoea II were found in July (Sherbakova and Korn 2011 and references therein).

The biology of an introduced species may differ in the non-native area compared to regions where the species has been established for longer periods (Brockerhoff and McLay 2011). Until recently, knowledge of where and when snow crab females in the Barents Sea release their larvae and at what time the different larval stages can be found in the water column has been limited. To our knowledge, the only previously published finding of snow crab larvae in the Barents Sea is by Dvoretzky and Dvoretzky (2019). They recorded snow crab zoea in plankton samples from the Eastern Barents Sea in the period between May 31st and July 8th 2013. The stage of the zoea was not reported. In the adjacent Kara Sea, zoea II were identified in planktonic samples in early October 2012 (Zimina 2014).

Two species of brachyuran crabs, *Hyas araneus* and *Hyas coarctatus*, were native to the Barents Sea prior to the establishment of the snow crab in the Barents Sea,

having a partly overlap in distribution with the snow crab (Zimina et al. 2015). Adult specimens can be readily distinguished, but more thorough examinations are needed on larval and juvenile stages (Pohle 1991; Ouellet and Sainte-Marie 2018; Zalota et al. 2018). Ouellet and Sainte-Marie (2018) included genetic analysis to verify the taxonomic identification.

Although the snow crab population is well established in the Barents Sea, no specific study on larval biology has been published. In the present study we describe findings of zoea stage I larvae of snow crab from central parts of the Barents Sea. They were both taxonomically and genetically verified. Time and location of hatching along with intermoult duration of the different larval stages have been unknown from the Barents Sea. This is vital knowledge for modelling further spread survival and recruitment of the snow crab population in the Barents Sea. The sampling of larva for this study was initiated on the basis of preliminary modelling of larval drift and survival in the area that is part of a study on the subject that is under preparation (Huserbråten et al. in prep).

Material and methods

A total of 23 vertical plankton hauls (station 1–23) were conducted during a snow crab survey targeting adult snow crabs in the central Barents Sea, June 22nd to July 3rd 2019, with the purse seiner M/S Talbor (Table 1). In the Barents Sea, the highest densities of snow crab are found in the central and eastern areas; therefore, sampling was concentrated in the eastern part of the survey area on a north–south transect along the delimitation line of the Barents Sea (Fig. 1). Six hauls were taken further north and west of transect. The survey area covered the Central Bank, the north-eastern Hopen Deep and southern parts of the Great Bank, all on the Norwegian continental shelf (Fig. 1). Depth at the sampling stations varied from 160 to 278 m.

A “WP3” (1000- μm mesh width; 1.0 m^{-2} mouth opening) was used for sampling plankton. The net was lowered to approximately 5 m above the seabed and then raised at a speed of approximately 0.5 m per second. However, there was no automatic speedometer on the winch that was used, so the speed might have varied somewhat between

the hauls. The plankton sample was sieved through a 500- μm net and stored in ethanol in 300 mL or 500 mL plastic bottles for further analysis in the laboratory. The sample from station 1 was contaminated and thus discarded from further analysis.

The plankton samples were mostly dominated by other species, such as *Calanus* spp., Appendicularia, Chaetognatha, Amphipoda and Hydrozoa, but only crab larvae were quantified. The snow crab larvae were identified, staged and counted for each station. Abundance of larvae is given as larvae per sample and per m^{-2} of sea surface, which was equal for all hauls as the net opening was 1 m^{-2} and the net was towed vertically. Bottom depth at each station is given in Table 1. Identification and staging of snow crab larvae were based on Pohle (1990), Korn et al. (2010) and Kornienko and Korn (2009). Morphometric data were obtained either from all or a maximum of 10 larvae from each station. The following morphological measurements were made: rostro-dorsal length (RDL), carapace length (CL), rostral spine length (RSL), dorsal spine length (DSL), eye width (EL) and eye height (EH) as described by Pohle (1991) (Fig. 2). All morphometric measurements were recorded by the same personnel using a stereomicroscope.

Table 1 Table of all sampling stations where the WP3 plankton net was used for vertical plankton sampling during the cruise to the Barents Sea in the summer of 2019

Station	Date	Time	Latitude	Longitude	Depth (m)	Number of snow crab larvae (m^{-2})
1	22.06.2019	04:30	N74° 31.80	E35° 32.40	275	–*
2	23.06.2019	15:12	N74° 40.80	E36° 35.40	230	3
3	23.06.2019	17:00	N74° 58.20	E36° 30.60	190	83
4	23.06.2019	20:15	N75° 21.60	E36° 58.80	166	143
5	27.06.2019	08:00	N76° 00.00	E37° 49.20	240	9
6	27.06.2019	23:30	N76° 15.00	E37° 21.60	278	21
7	28.06.2019	10:20	N76° 42.00	E37° 07.20	207	0
8	28.06.2019	22:00	N76° 48.00	E35° 58.20	180	3
9	29.06.2019	09:00	N76° 28.20	E36° 06.00	270	0
10	29.06.2019	19:15	N76° 03.60	E36° 16.80	250	8
11	29.06.2019	20:55	N75° 58.20	E35° 42.00	222	3
12	01.07.2019	08:10	N76° 09.00	E35° 07.20	276	3
13	01.07.2019	15:15	N76° 09.00	E37° 13.80	263	5
14	01.07.2019	22:30	N76° 13.80	E37° 44.40	278	1
15	02.07.2019	08:40	N75° 56.40	E37° 55.20	235	21
16	02.07.2019	10:40	N75° 48.00	E37° 43.20	207	69
17	02.07.2019	11:52	N75° 39.00	E37° 32.40	187	45
18	02.07.2019	13:15	N75° 30.60	E37° 22.20	165	60
19	02.07.2019	14:20	N75° 22.80	E37° 11.40	160	24
20	02.07.2019	16:00	N75° 13.20	E37° 01.80	182	60
21	02.07.2019	17:30	N75° 04.80	E36° 52.20	170	4
22	02.07.2019	19:05	N74° 56.40	E36° 42.00	208	27
23	02.07.2019	20:30	N74° 48.00	E36° 42.00	200	9

The rightmost column gives the number of snow crab (*Chionoecetes opilio*) larvae in the sample

*The sample from station 1 was contaminated and could not be counted

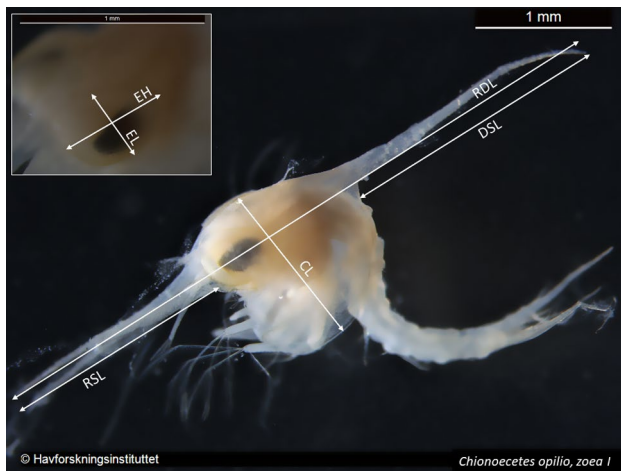


Fig. 2 Photograph of wild caught snow crab (*Chionoecetes opilio*) zoea I with illustration of the different measurements taken. *RDL* Rostradorsal length, *CL* Carapace length, *DSL* Dorsal spine length, *RSL* Rostral spine length, *EH* Eye height, *EL* Eye length

From each station, either all or a maximum of five larvae were selected for molecular verification using a 710 bp fragment of the mitochondrial COI gene with the primers LCO1490 and HCO2198 (Folmer et al. 1994). DNA was isolated from the whole larvae using Qiagen Blood and Tissue kit (Qiagen N. V, Germany), following the manufacturer's protocol. PCR was performed in a 10 μ L reaction volume with 2 μ L of template DNA, 5 μ L Qiagen multiplex kit and 0.25 μ L of each of forward and reverse primer (10 μ M) and adding up with dH₂O to a final reaction volume of 10 μ L. The PCR was carried out on a MiniAmp thermal cycler (Thermo Fisher, USA) with a temperature profile of 95 °C for 15 min; 35 cycles of 95 °C for 60 s, 48 °C for 60 s and 72 °C for 60 s; 72 °C for 10 min. PCR products were sequenced bidirectionally using the same primers as in the initial PCR. The sequencing was carried out on an ABI 3500 genetic analyser using the BigDye v3.1 chemistry following the manufacturer's instructions (Thermo Fisher, USA). Sequences were assembled, aligned and quality checked using the software Geneious Prime (Biomatters, Ltd, New Zealand). Subsequently the sequences were uploaded to the NCBI database and species identification was done through the MegaBLAST algorithm (Morgulis et al. 2008).

All statistical and graphical presentations of the data were carried out using R software (R Core Team 2018).

Results

All of the 601 Majid larvae recorded in the samples were taxonomically identified and staged to zoea I snow crab. The result from the molecular validation unequivocally matched all analysed larvae to snow crab with an identity

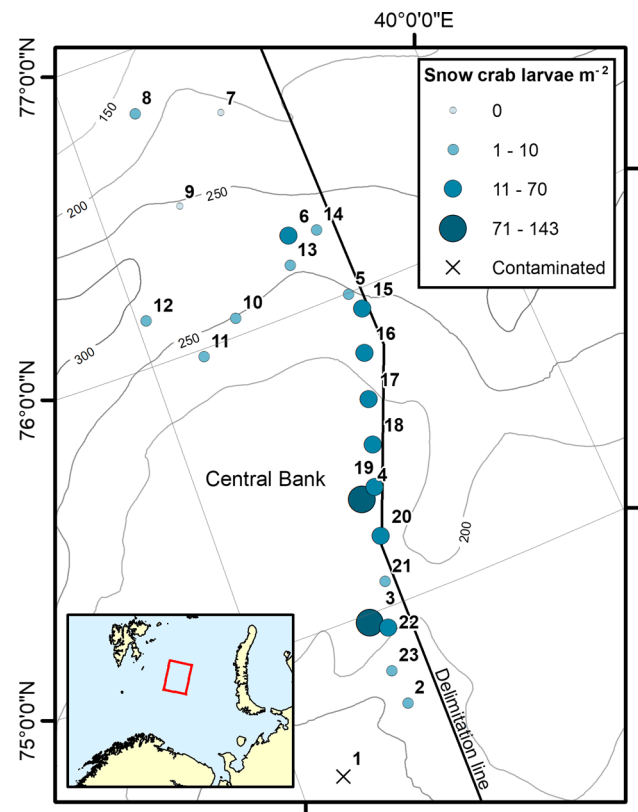


Fig. 3 Map showing the stations (blue points) sampled for planktonic larvae during the snow crab survey. The size of the point reflects the abundance of snow crab (*Chionoecetes opilio*) zoea I larvae per m^{-2}

to the NCBI reference sequences ranging from 97 to 100% (96–98% coverage). 79% of the sequences were matched to either accession no MG321135 (60%) or MG321144 (19%). Snow crab zoea II or megalopa was not found in any of the samples.

Snow crab larvae were present in 20 of the 22 samples collected over a period of ten days (Table 1). The highest abundance (143 m^{-2}) was observed above the Central Bank (Fig. 3). At 40% of the stations more than 20 larvae were found. The number of larvae ranged from 0 to 143 individuals with a mean of 27 (SD \pm 36) per m^{-2} .

Mean rostradorsal length (RDL) of the larvae was 4.93 mm (SD \pm 0.18), mean dorsal spine length (DSL) was 1.98 mm (SD \pm 0.13), mean rostral spine length (RSL) was 1.71 mm (SD \pm 0.11) and mean carapace length (CL) was 1.25 mm (SD \pm 0.07). Eye measurements were 0.57 mm (SD \pm 0.03) mean height (EH) and 0.36 mm (SD \pm 0.03) mean length (EL) (Table 2). All our measurements were in accordance with results in Pohle (1991) (Fig. 4).

In agreement with Pohle (1991), we experienced that RDL was the most robust morphological measurement, whereas CL, EL and EH were more difficult and could not

Table 2 Mean and standard deviation morphological measurements of zoea I larvae of snow crab (*Chionoecetes opilio*) from the Barents Sea compared with Pohle 1991 (Table 2) and other studies

Study	Location	n	Larvae source	Morphometric measurements in mm:						Latitude
				RDL	CL	DSL	RSL	EH	EL	
Current study	Barents Sea	124	W	4.93±0.18	1.25±0.07	1.98±0.13	1.71±0.11	0.58±0.03	0.36±0.03	N76°
Pohle (1991)	NW Atlantic	50	L	4.92±0.17	1.33±0.08	2.12±0.13	1.72±0.10	0.57±0.03	0.35±0.03	N48°
		10	W	4.90 (4.70–5.08)	1.28 (1.19–1.44)	1.97 (1.84–2.16)	1.67 (1.58–1.87)			
Korn et al. (2010)	Sea of Japan		W	5.04±0.18	1.02±0.07					N39.6°
Webb et al. (2006)	Eastern Bering Sea	6	L	4.55±0.16		1.95±0.07	1.70±0.06			N58°
Ouellet and Sainte-Marie (2018)	Gulf of St. Lawrence		W & L							N48°
	North GSL			4.51±0.38	1.21±0.08					
	South GSL			4.40±0.53	1.16±0.14					

RDL Rostrodorsal length, CL Carapace length, DSL Dorsal spine length, RSL Rostral spine length, EH Eye height, EL Eye length. Larvae source is coded as W (wild caught) or L (Laboratory hatched)

be obtained confidently from every specimen because of damages caused by sampling.

Discussion

All the Majid crab larvae found in the plankton samples in the current study was, using taxonomic identification and molecular analysis, verified to be snow crab zoea stage I larvae. All of the morphological structures measured fitted well within size ranges reported for zoea I in Pohle (1991), and our results also fits well with measurements from other studies on laboratory reared and wild caught snow crab larvae from different geographical areas and latitudes (Table 2).

Adult specimens of snow crab and *Hyas* spp., belonging to same family (Oregoniidae), are readily separated. However, morphological similarities in larval stages makes them challenging to distinguish (Roff et al. 1984; Pohle 1991; Ouellet and Sainte-Marie 2018) and in the Barents Sea area, both *H. araneus* and *H. coarctatus* are common (Dyer 1985; Zimina et al. 2015). The extent of temporal and spatial co-occurrence of larval stages of snow crab and *Hyas* spp. in the Barents Sea is unknown. Weslawski (1987) reported pelagic occurrence of zoea larvae of *H. araneus* in the period April to August from southern Spitsbergen. From the northern Norwegian coast, Michelsen et al. (2020) report that *H. araneus* releases their larvae as early as March and latest in June, whilst *H. coarctatus* was observed to release larvae later in the spring (May–June). Further, Dvoretiskii (2011) reported findings of *H. araneus* zoea stage I and II during three days in the period 30th May to 1st June in coastal areas of southern Barents Sea. From these reports and the findings of snow crab larvae in both June and July reported in this study, we expect there to be some co-occurrence of *Hyas* spp. and snow crab larvae in the Barents Sea. However, adult stages of *Hyas* spp. are likely more abundant around the Svalbard archipelago and in the Goose Bank areas (Zimina et al. 2015), compared to the area covered in this study. This might explain the lack of *Hyas* spp. larvae in our samples. Co-occurrence of larvae of the different species might be taking place in other areas of the Barents Sea where *Hyas* spp. is more abundant. Sizes of *Hyas* spp. larvae varies and might overlap with the size of snow crab larvae (Pohle et al. 1991 and references therein), particularly zoea I of snow crab and zoea II of *Hyas* spp. might be similar in size. If differentiation of the species through taxonomic identification is difficult, we recommend continue using molecular validation to aid identification also in future studies to reveal potential co-occurrence. If such was to be found in the Barents Sea, the potential for separating them based on size (as shown by e.g. Pohle (1991)) should be investigated further.

During our survey, adult females were also collected. Amongst the multiparous females sampled, most individuals

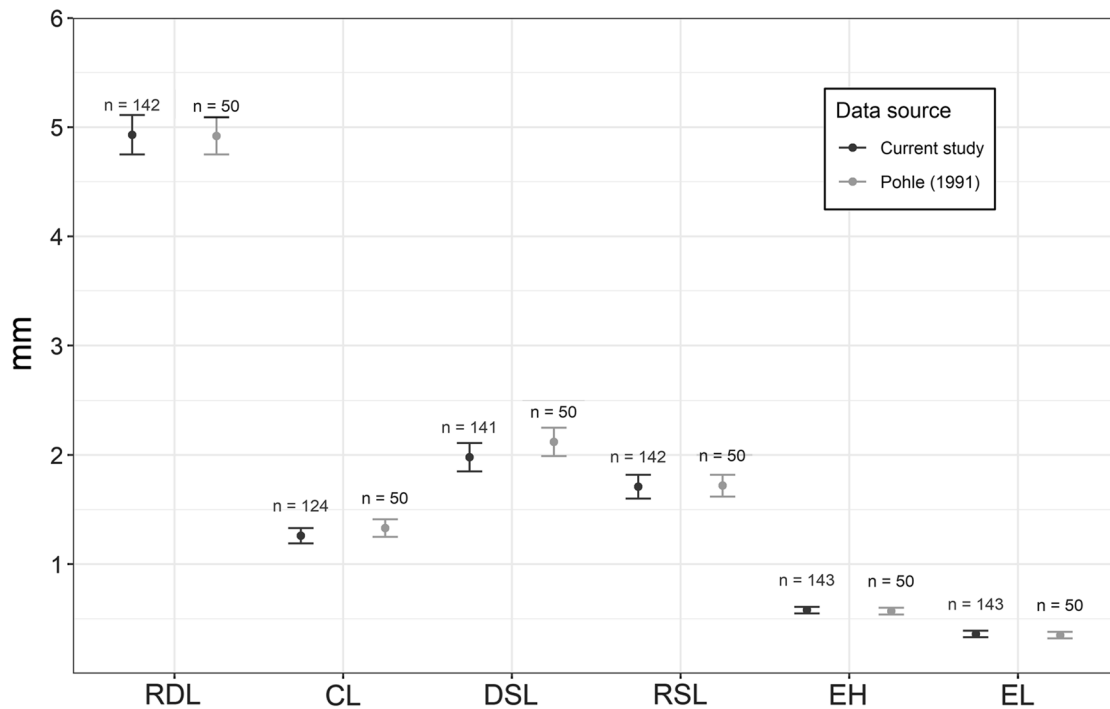


Fig. 4 Illustration of Table 2 Mean and standard deviation of all the morphological measurements of zoea I larvae of snow crab (*Chionoecetes opilio*) from the Barents Sea compared with Pohle (1991). Number of larvae *RDL* Rostradorsal length, *CL* Carapace length, *DSL*

Dorsal spine length, *RSL* Rostral spine length, *EH* Eye height, *EL* Eye length. The measurements are illustrated and described in Pohle (1991)

(96%) had recently spawned (bright orange) eggs, but also females with late stage- and recently spent eggs were found. This suggests that larval release and mating was ongoing during the sampling period, as multiparous females mate shortly after hatching of the eggs (Conan and Comeau 1986). This is further supported by the lack of zoea II in our samples. The temporal spread of larval hatching in Barents Sea snow crab is so far unresolved. Timing of larval release for benthic invertebrates can be triggered by external cues like temperature, light/dark regimes, lunar and tidal cycles, presence of food or a combination of several factors (Thorson 1950). For snow crab, several theories about the cue for hatching have been discussed (Emond et al. 2020). Hatching is proposed to be initiated by the presence of senescent phytoplankton settling through the water column, so that hatching overlaps with post-plankton-bloom when diatoms and copepod nauplii are present as prey for the newly hatched crab larvae, thus increasing survival rate (Kruse et al. 2007). We know that hatching in native areas can start as early as in February in Sea of Japan (Kon et al. 2003) or as late as June as in Sea of Okhotsk (Sherbakova and Korn 2011). The hatching period of snow crab is proposed to last over a period of as much as three months (Kon et al. 2003; Kuhn and Choi 2011). Newly hatched larvae rapidly rise in the water column and during the zoea stages the snow

crab remains distributed within or above the pycnocline in the stratified water column (Starr et al. 1994; Ouellet and Sainte-Marie 2018). Thus, the temperature regime in the upper water masses regulate intermoult duration of the larvae as it is closely related to temperature (Shcherbakova and Korn 2011; Webb et al. 2007; Yamamoto et al. 2014; Ouellet and Sainte-Marie 2018). Ouellet and Sainte-Marie (2018) propose a modelled relationship between temperature and intermoult duration based on several laboratory studies of snow crab larvae. According to the modelled relationship, the duration of the first zoea stage is 126 days at 1 °C and 71 days at 3.5 °C. However, the study also showed that in the laboratory experiments, larval mortality at temperatures lower than or equal to 3 °C was 100%.

In the Barents Sea, the stabilization of the upper water mass layer established in late April or early May stratification usually is strengthened in March and April due to solar heating which results in onset of the phytoplankton bloom (Loeng 1991; Dong et al. 2020). In a study using data from the Central Barents Sea from August to September in the period 1970 to 2016, temperatures in the upper water masses roughly ranged from 1 to 3.5 °C and the pycnocline generally establishes around 50 m (Lind et al. 2018). A study by Dvoretzky and Dvoretzky (2019) found snow crab zoea in Barents Sea water masses east of our study area in June and

July 2013. They reported that the water masses had a vertical stratification at 40–60 m and the temperature in the upper water layers ranged from 0.5 to 2.5 °C, which is in accordance with the study by Lind et al. (2018).

Given an intermoult duration from zoea I to zoea II according to the modelled relationship proposed by Ouellet and Sainte-Marie (2018) one would expect to observe the first zoea II larvae 71 to 126 days after hatching in our area, given the temperature range 1 °C to 3 °C. The lack of zoea II in the samples suggests that hatching had occurred no more than 125 days earlier, around the middle of February. According to Ouellet and Sainte-Marie (2018) survival from zoea I to zoea II is expected to be very low or zero at such low temperatures. If hatching do occur as early as February and March in the Arctic Barents Sea we expect the survival of those larvae to be extremely low due to unfavourable conditions, such as low temperatures, sea ice cover and limited food availability. The lack of zoea stage II in our samples may be caused by high mortality amongst early hatched larvae or that hatching in the Barents Sea in fact do starts later in the season. Following the same reasoning as above, zoea I that hatched in late June or in the beginning of July might not moult to zoea II until the end of October. In the Kara Sea (adjacent to the Barents Sea) zoea stage II has been recorded in planktonic samples in early October (Zimina 2014).

Larval dispersal depends on local currents systems (Parada et al. 2010; Mao et al. 2019). The properties of water masses (such as temperature) above the hatching site will affect the duration of the larval phase. As the exact time since hatching is unknown in our study, determining where the larvae were hatched is challenging given that they would have been transported with water currents for an unknown period. Modelling larval drift from a given release sites might give insight to the duration of the larval phase. Such studies are presently in progress (Huserbråten et al. in prep). Our sampling was conducted during the hatching period and we presume that the larva had not been advected far from the hatching site.

Given the abundance of reproducing snow crab in the sampling area, larvae were expected to be numerous in plankton samples. From the northern Gulf of St. Lawrence, Ouellet and Sainte-Marie (2018) report mean abundance of snow crab larvae zoea I to be 17.76 ± 14.9 zoeae m^{-2} in late May 2002, and from the Bering and Chukchi Seas, Landeira et al. (2017) report mean abundance of zoeal stages to be 42.91 ± 93.26 zoeae m^{-2} in June and July 2008. The abundance found in our study was 27 ± 36 larvae per m^{-2} which is comparable with those reported elsewhere. Stations with highest abundance of larvae were located over the Central Bank at relative shallow depth of 195 m. Stations with few or zero larvae, where generally located north and south of the bank area. Higher abundances of larvae found over the bank area may be caused by favourable conditions, such as

high densities of prey or retention caused by local hydrographical patterns.

Conclusion

This study confirms presence of snow crab zoea I in the Central Barents Sea during the end of June and the beginning of July 2019. Misidentification of *Hyas* spp., as snow crab was ruled out, supported by genetic analysis. It seems like snow crab and *Hyas* spp. larvae do not overlap spatially in our study area or might not have the same planktonic period. This may, however, appear, when the snow crab continues spreading further west into areas where *Hyas* spp. are more common. In the future, Barents Sea larvae from both snow crab and *Hyas* spp. should be compared to reveal potential size differences. No snow crab zoea stage II was found. Based on the timing of our survey and knowledge from the literature we can assume that the snow crab females in the Barents Sea had recently released their larvae or was in the process of doing so during the sampling period. Timing of hatching and larval survival will also be input to model the potential further spread of the population by means of larval dispersal. Our findings may serve as a starting point for further investigation into the snow crab larvae biology in the Barents Sea, e.g. investigations of a possible relationship between egg production and recruitment to the fisheries. The current study was limited in its spatial and temporal coverage. Further studies with better spatial and temporal coverage are needed to determine the onset, peak and duration of the hatching period in the Barents Sea and increase understanding of reproduction and recruitment in the snow crab population in the Barents Sea.

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Author contributions AMH and HEHD designed the sampling regime and performed the collection of data. AMH, HEHD and ALA did the sorting of material and identification of the larvae. HEHD performed the measurements of the identified larvae. JIW was responsible for the molecular analysis. AMH, HEHD and ALA wrote most of the manuscript and JIW supplemented regarding the molecular analysis. All authors have read and approved the manuscript.

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Data availability The cruise data are available through the Institute of Marine Research (IMR) data centre. <https://www.hi.no/hi/forskning/forskningsgrupper/norsk-marint-datasenter-nmd>.

Declarations

Conflict of interest The authors have no affiliation with any organization with a direct or indirect financial interest in the subject matter discussed in the manuscript. Here it could be the snow crab fishery ongoing in the Barents Sea. The institute main aim is to give the best advice to the government for a sustainable fishery.

Ethical approval Permission to conduct fishery was given by the Directorate of Fisheries. The permission letter is attached. All methods used are in accordance with ethical guidelines of IMR.

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